

# ***Homo sapiens* is the apex animal: anthropocentrism as a Dionysian sword**

**Peter JS Fleming<sup>1,2</sup> and Guy Ballard<sup>1,3</sup>**

<sup>1</sup>Predators, Prey, Plants and People Project, School of Environmental and Rural Sciences, University of New England, Armidale, NSW 2351, Australia.

<sup>2</sup>Vertebrate Pest Research Unit, Biosecurity NSW, NSW Department of Primary Industries, Orange Agricultural Institute, Forest Road Orange, NSW 2800, Australia.

<sup>3</sup>Vertebrate Pest Research Unit, Biosecurity NSW, NSW Department of Primary Industries, Ring Road North, Armidale, NSW 2351, Australia.

## **ABSTRACT**

Anthropocentrism, where humans are central, is a natural human viewpoint, but a threat to objective ecological study. Human population, resource use and resource expectations are expanding, turning our ecological footprint into a deep rut. We believe that, while many studies deal with the consequences of human effects on ecosystems, the outcomes are viewed as if humans were observers rather than participants in ecosystems.

Humans are the apex animal, manipulating most ecosystems with forestry, mining, agriculture, manufacturing and urbanisation: we engineer the landscape, the air, the water and even the climate. In many situations, humans are also the top predator, killing both our competitive mesopredators and their herbivorous prey. Leaving the top predator out of models reduces the alternative hypotheses and imposes directional bias on the responses of subordinate trophic levels. Our objective here is to discuss the roles of the human in the room and the consequences of ignoring them when designing experiments, proposing explanatory models and interpreting studies.

**Key words:** agri-ecosystem, apex predator, climate change, dingo, ecosystem engineer, fox, livestock, rabbit, water

DOI: <http://dx.doi.org/10.7882/AZ.2015.019>

## **Introduction**

King Dionysius II and Damocles had a deal. They would switch places for a day so that the unctuous Damocles could experience the wealth, luxury and power that went with sitting on a 4<sup>th</sup> Century Sicilian tyrant's throne. However, Dionysius suspended his large sword above the throne by a single horse hair. This dampened Damocles' enthusiasm for fortune and authority; it was too much for him, so he fled.

How does this idea, which was demonstrably dangerous for Damocles, relate to anthropocentrism? By regarding and interpreting life from the viewpoint of human values and experiences, we humans place ourselves at the centre of our world. Our natural view of the world is from our perspective, where surrounding ecosystems are there to provide us with resources for consumptive and non-consumptive use. The danger in the idea comes when, through anthropocentrism, we mentally separate ourselves from nature and forget that we are biological entities. Despite broad acceptance that humans are the greatest ecosystem engineers among all animal species, zoologists and ecologists often ignore the consequences of those impacts in explanatory models for ecosystem function. We devise neat

experimental designs with some treatment sites and some nil-treatment sites, but when we come to explain the measured differences between the two, we often assume that human impacts are constant across sites. By not including humans and their effects in models, we will never gain necessary understanding about system function or have the capacity to predict the outcomes of management. Ecology is simply the study of organisms and their interactions with everything in their environment; so, studying ecology sans human impact is not really studying ecology at all. This, then, is the Dionysian sword that hangs over ecologists and land managers.

Therefore, the objectives here are fourfold. First, we outline why we ascribe apex consumer and engineer status to humans. Second, we identify the past and current roles of humans in Australian ecosystems and the possible impacts of ignoring this Dionysian sword. Thirdly, we examine the consequences of including humans in models for restorative actions. Finally, we provide direction for including human effects that might change the way studies are designed, undertaken and analysed, and the conclusions that are drawn from them.

## Welcome to the Anthropocene: humans are the apex ecosystem engineers

This is not news. In the current time, termed the "Anthropocene Epoch" (Crutzen 2006), humans have become the dominant vertebrate. To meet the needs of increasing human populations and their demands for improved standards of living, our technology is increasingly complex and dominates other species. No other animal has the same impact on ecosystems. Humans manipulate the landscape by farming, grazing, forestry, introducing invasive plants and animals, roading, urbanisation, clearing, irrigating, damming, mitigating floods, manufacturing and polluting. We have even modified the fauna and flora to our purposes through domestication. We move plants and animals about the globe, effectively joining landmasses that have been separated since the melting of the last Ice Age. If we need water, we build dams and weirs that alter stream flows and salinity levels. To cross waters and terrain that were once barriers, we build bridges and tunnels. The most insidious anthropogenic pollution is the production of greenhouse gasses, which affects climate and weather. In the Anthropocene epoch, we are no longer passengers on the earth: we are its drivers (Hobbs *et al.* 2006).

## Humans are the apex predators

Humans are the apex predator in that they fill the top trophic position (Buskirk 1999; Fleming *et al.* 2012) in most ecosystems. This is particularly so in agri-ecosystems, but also applies wherever humans kill animals for food, ecological and agricultural damage mitigation, or recreation.

As omnivores and generalist predators, humans eat seeds, grasses, herbage and fruit, and prey upon everything from insects to elephants and whales. Although smaller than much of their prey suite, humans have been able to use technology, hunting in groups, and hunting and herding aids such as horses and dogs to capture and kill large prey. The raising of livestock allows predation on a large scale and ensures continuity of food supply. By domesticating ungulates, much of the risk was removed from the hunting process. The development of traps and firearms enabled prey to be killed from a distance with little or no danger to the predator.

The best evidence that *Homo sapiens* is the apex predator is that humans have been responsible for the endangerment and extirpation of terrestrial large carnivores, mostly since the 1800s (Hayward *et al.* 2007; Woodroffe 2000; Zimmermann *et al.* 2009). This is particularly so for those with more specialised diets; for example, wolf density is negatively correlated with human density and anthropogenic loss of habitat (Linnell *et al.* 2001; Woodroffe 2000).

## A brief history of human impacts in Australia

The impacts of humans on landscapes have been through the management of fire, introduction of forage plants, weeds, ornamentals and crop plants, introduction of domesticated and other animals, introduction of novel pathogens, the harnessing and polluting of water, the ecological blitzkrieg of urbanisation, and imposition of built infrastructure for energy, transportation and extractive industries. All these have progressively changed the landscape, with the greatest impacts being since the advent of Europeans.

The underlying aridity, stochasticity of rainfall and limited distribution of permanent waters over much of the Australian continent led to the evolution of fascinating fauna able to respond to brief periods of overwhelming feast interspersed with long periods of famine. Humans have been in Australia for at least 45,000 years (Bird *et al.* 2013) and occupied most ecosystems, albeit at varying densities attributable to carrying capacity. During human occupation, there have been subtle and obvious impacts on the various ecosystems on the continent. In that time, there have also been an Ice Age and its subsequent Holocene epoch, which separated Tasmania and Kangaroo Island from the mainland about 10-12,000 years ago. Indigenous humans modified many of the ecosystems to promote year-round supplies of food (Gamage 2011). It is likely that their burning regimes prepared the way for the introduction of domestic ungulates by Europeans, with much of the landscape described as "an English nobleman's park" (Smith 1960, p. 133-134).

Asian and European people have introduced non-indigenous animals and the first, the dingo *Canis familiaris* (see Jackson and Groves 2015), a eutherian carnivore imported from South East Asia about 4000 years ago (Corbett 2001; Oskarsson *et al.* 2012; Pang *et al.* 2009; Savolainen *et al.* 2004) that likely had major impacts on fauna (Johnson 2006). Today, dingoes and other wild dogs likely limit abundance and distribution of native fauna including macropods (Macropodidae) and emus (*Dromaius novaehollandiae*) (Choquenot and Forsyth 2013; Jonzen *et al.* 2010; Pople *et al.* 2000).

The next major anthropocentric changes began after 1788 when Anglo-Europeans constructed a penal colony at Port Jackson, and settlements in Tasmania (1803-04), Victoria (1835), South Australia (1836) and Western Australia (1826-29). European impacts accelerated with the crossing of the Blue Mountains in 1813 and a press to take agriculture to the "interior" after 1815 (Atkinson 1826). The clearing of lands to create an agricultural landscape more like England was promoted in the Colony of New South Wales, which included present-day Victoria and Queensland, and this was facilitated in the interior and north along the Great Dividing Range from Sydney

and Newcastle by deployment of convicts armed with axes. From the 1830s, livestock production expanded from Port Phillip into the Western and Wimmera Districts of Victoria, corresponding with the dispossession of the local indigenous people (Letnic 2000) and changes to fire regimes likely resulted (Gamage 2011).

The same water limitation that was the major restrictor of spatial dispersion of people likely resulted in correspondingly low dingo abundance away from the permanent water holes. Rapid uptake and spread of Australian merino sheep (*Ovis aries*) and cattle (*Bos* spp.) throughout the Western Districts of Victoria, the Murray-Darling floodplains (Williams 1962; Lunney 2001) and the downlands of southern and central Queensland (Bauer 1962) from 1830-1860, was, however, initially constrained by the distribution of permanent water. That was until the tapping of the Great Artesian Basin after the first bore was sunk near Bourke, NSW in 1878. Major earthworks and sinking of bores were necessary for livestock production in localities away from the river systems (Williams 1962). As these developments followed extirpation of dingoes in much of the semiarid rangelands, it is likely that the current density of kangaroos (*Macropus* spp.) and feral goats (*Capra hircus*) south and east of the Dingo Barrier Fence is a response to water availability more so than removal of predation. The current increasing abundance of feral goats in the Western Division of NSW (Ballard *et al.* 2011) and the independence of kangaroo densities from culling quota off-take (Lunney 2010; Wilson and Edwards 2008) show that humans are not always effective predators. These facts, and the dispersion of sheep and rabbits (*Oryctolagus cuniculus*), show that reintroduction of dingoes would be on a vastly different landscape canvas to pre-European occupation and influence (Allen 2011; Fleming *et al.* 2012).

The impact of European agriculturalists on Australian landscapes was immense and relatively sudden (Allen 2011; Lunney 2001). Negative impacts of overgrazing on grasslands were observed early (Atkinson 1926) and repeated wherever livestock and rabbits went (Butlin 1962; Williams 1962). In the Western Division of New South Wales, sheep numbers increased from 354,000 in 1860 to 13.6 million in 1891, with numbers tripling from 1879 (Butlin 1962). Between 1895 and 1904, sheep numbers crashed to 3.6 million in response to drought and overgrazing by sheep and rabbits (Butlin 1962). Likewise, but later, in the north of Australia, the sinking of bores through the 1960s and on, provided cattle with greater access to grassland ecosystems (Hunt *et al.* 2007), which were supplemented with introduced grasses and altered fire extent and intensity (Rossiter *et al.* 2003). The vegetation changes that resulted from these catastrophic anthropogenic forces persist. This is evidenced by the dramatic re-emergence of many semi arid plant species after the escape and success of rabbit haemorrhagic disease (RHD) in the late 1990s (Bird *et al.* 2012; Saunders *et al.* 2002), the increases of some small mammal

densities in northern Australian systems after removal of cattle (Legge *et al.* 2011) and, conversely, in the hotter and more widespread fire regimes of the north (Woinarski *et al.* 2004; Woinarski *et al.* 2011). The major changes to grassland ecosystems caused by livestock overgrazing may not be reversible (e.g., South Africa, Archer 2000; North America, Fleischner 1994; Tibet, Fleming *et al.* 2013) and hence need to be considered as anthropogenic drivers of faunal biodiversity change.

Permanent water is now a feature of semi-arid and arid rangelands and few places are further than 10 km from water (Fensham and Fairfax 2008; Hacker and McLeod 2003). The effect of this change on the distribution of plants and animals (Hunt *et al.* 2007) should not be undersold. Gross structural and floristic changes to vegetation form piospheres radiating from focal water points (Derry 2004; Lange 1969), with productivity and structural diversity of the vegetation and associated faunal assemblages decreasing concentrically towards the focus (but see contrary opinion in Wallach and O'Neill 2009). In Western NSW, parts of semi-arid central and southern Queensland and southern South Australia, kangaroos (particularly reds, *M. rufus*) and feral goats have benefitted from these changes (Ballard *et al.* 2011; Caughley and Grigg 1982; Caughley 1986; Caughley *et al.* 1980; Hacker and McLeod 2003) and the extirpation of dingoes and exclusion (by the Dingo Barrier Fence) associated with the introduction of sheep (Allen and West 2013).

However, the underlying conditions on either side of the Fence are also likely associated with gross differences in landuse by agricultural humans over the past 100 years. There are inherent differences in landscape productivity recognised by early administrators, such as Goyder in South Australia when determining the distribution of sheep rangelands, and more recently by Newsome *et al.* (2001). These differences have likely been exacerbated through the 100 years of different livestock enterprises and herbivore combinations, particularly by the combination of sheep and rabbits to the south and east of the Fence. The importance of overgrazing by sheep and rabbits, as causes of small mammal extinction in Western Division of NSW, are well documented (e.g. Letnic 2001; Lunney 2001; Williams *et al.* 1995). Without accounting for the underlying differences on either side of the Fence, studies (e.g., Letnic *et al.* 2009; Letnic and Koch 2010; Letnic and Dworjanyn 2011) are likely to draw erroneous conclusions about dingo effects on fox distributions. An alternative and more parsimonious explanation for higher fox density to the south and east of the Fence is that the distribution and density of foxes is more or less aligned with anthropogenic prey subsidies. This includes the Australia-wide distribution of rabbits (Saunders *et al.* 1995, West 2008), which are a primary prey of foxes in their native range (Saunders *et al.* 1995), and higher historical (Butlin 1962; Allen 2011) and current (Australian Bureau of Statistics 2009) sheep densities.

*Homo sapiens* is the apex animal

Dams and tanks, and pasture changes with artificial fertiliser and productive introduced grasses and legumes have greatly increased the livestock stocking rates in the higher rainfall zones. Although some fauna there likely benefited from anthropogenic influences (e.g., sulphur crested cockatoos-*Cacatua galerita*, wood ducks- *Chenonetta jubata*, eastern grey kangaroos *Macropus giganteus*, brush-tailed possums *Trichosurus vulpecula*), others most definitely haven't (e.g., koalas *Phascolarctos cinereus* in NSW, Lunney *et al.* 2007 ; yellow-footed rock-wallabies *Petrogale xanthopus*, Lethbridge and Alexander 2008).

Biodiversity has decreased substantially across the wheat / sheep zones of southern and eastern Australia, where clear-felling of woodlands and forests and often laser levelling of land has preceded the planting of crops for human and livestock consumption. Human-made monocultures include grasses (wheat and sugar cane), forbs (e.g., canola and lucerne), shrubs (e.g., tea tree *Melaleuca alternifolia* and macadamia *Macadamia integrifolia*) and trees (e.g., *Pinus radiata* and *Eucalyptus globulus*), and are usually depauperate of fauna by comparison with structurally intact ecosystems (Brockhoff *et al.* 2008).

Introduced invasive animals provided the next major anthropogenic engineering effect on Australian landscapes. Rabbits spread north and west from their introduction point in Geelong in 1859 (Coman 1999) and their rapid expansion into the semi-arid sheep rangelands was probably facilitated by the pioneering spread of sheep. Rabbits are renowned for causing vegetation change and erosion (Croft *et al.* 2002; Eldridge and Simpson 2002; Mutze *et al.* 2008). The spread of European red foxes (*Vulpes vulpes*) was likely facilitated by the prior spread of rabbits, and their current distributions are correlated (Saunders *et al.* 2010). Goats were introduced in 1788 and became feral with the failure of early angora mohair and cashmere industries in the 1830s (Evans 1980; Harrington *et al.* 1982). However, while they likely had local impact on fauna (e.g., yellow-footed rock-wallabies, Lethbridge and Alexander 2008), their numbers did not really escalate until the 1990s (Ballard *et al.* 2011) and their impacts are largely unmeasured.

Nevertheless, the combination of sheep, cattle, goats, rabbits and kangaroos, have caused gross anthropogenic engineering to semi-arid ecosystems, even affecting soil carbon and microbial activity (Holt 1997). Although RHD reduced rabbit populations over much of their distribution, grazing and browsing pressure from all large herbivores continue to restrain vegetation recovery (Denham and Auld 2004) and livestock are more likely to cause irreversible vegetation change than communities that are not anthropogenically controlled (Van De Koppel and Rietkerk 2000).

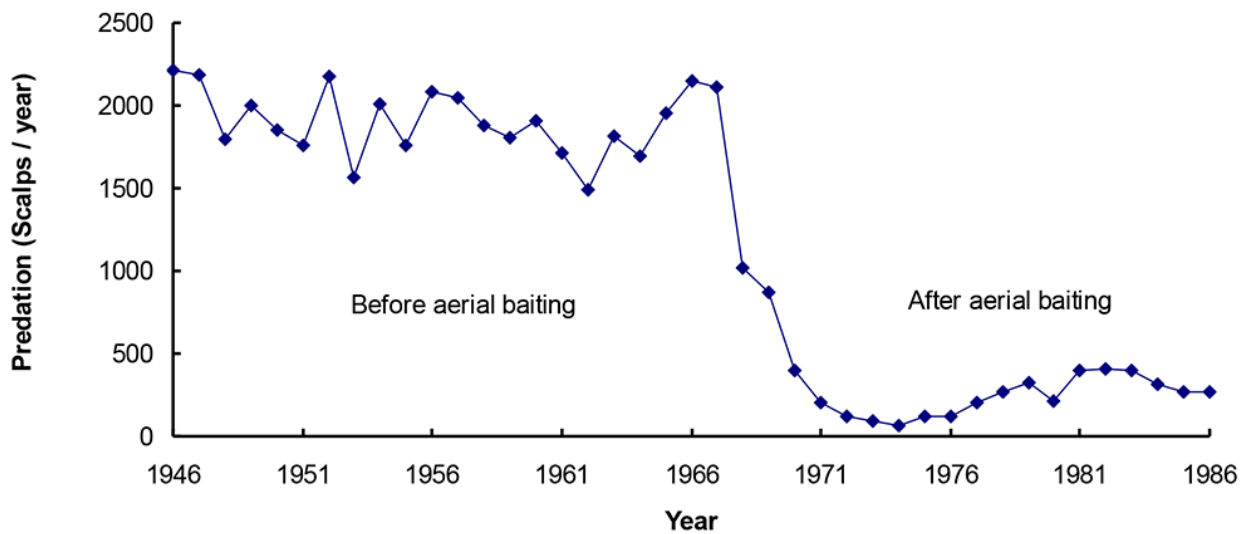
Red foxes and feral cats (*Felis catus*) are notorious examples of destructive animals purposely and accidentally released by humans (Lapidge and Henshall 2001; Meek and Triggs 1998; Abbott 2002). These predators modify faunal assemblages (Burbidge *et al.* 2009; Dickman *et al.* 2009; Read and Bowen 2001) and are linked to zoonoses and diseases affecting wildlife (Fleming *et al.* 2014; Jenkins *et al.* 2005; Saunders *et al.* 2010).

The greatest anthropogenic changes in Australia have likely occurred in the past 50 years. The human population is concentrated along the east and southern coasts of the continent and 73% live in capital cities (Australian Bureau of Statistics 2012). The population has doubled in the past 50 years (Australian Bureau of Statistics 2014) and is associated with gross landscape changes through urbanisation, industrial development, forestry, open cut mining, and intensive agricultural industries, such as market gardens, dairying and poultry production. Rapid increase in the human population and their ecological footprint has also led to fragmentation of forests and woodlands with potentially great impacts on ecosystem flux (Gill and Williams 1996).

## Humans are the top-order predators in Australia

Indigenous and traditional hunting (predation) on wildlife populations is practiced across the world (Redford and Sanderson 2000), as are recreational hunting and commercial hunting (e.g., kangaroos, Thomsen and Davies 2005, and deer in Australasia, Bauer and Giles 2002; Nugent and Choquenot 2004). Indigenous Australians have always been predators and their continental occupation coincided with the now-extinct megafauna for about 30,000 years (Wroe *et al.* 2004). Indigenous Australians manipulated landscapes with burning to reduce vegetation density to aid movement and hunting, and to provide grazing lawns to attract macropods (Atkinson 1826; Gamage 2011). Wombats (Vombatidae) ("its flesh is good eating being very fat", Atkinson 1826, p 25) and bilbies (*Macrotis* spp.) were dug out of burrows, and koalas ("which appear to be a delicate meat", Atkinson 1826 p25) were easily captured with throwing sticks (Moyal 2008). Since European occupation, Australians have preyed upon kangaroos, possums and koalas for their skins (Moyal 2008), and kangaroos are still hunted for consumptive use and agricultural damage mitigation (McLeod *et al.* 2004; Pople *et al.* 2010).

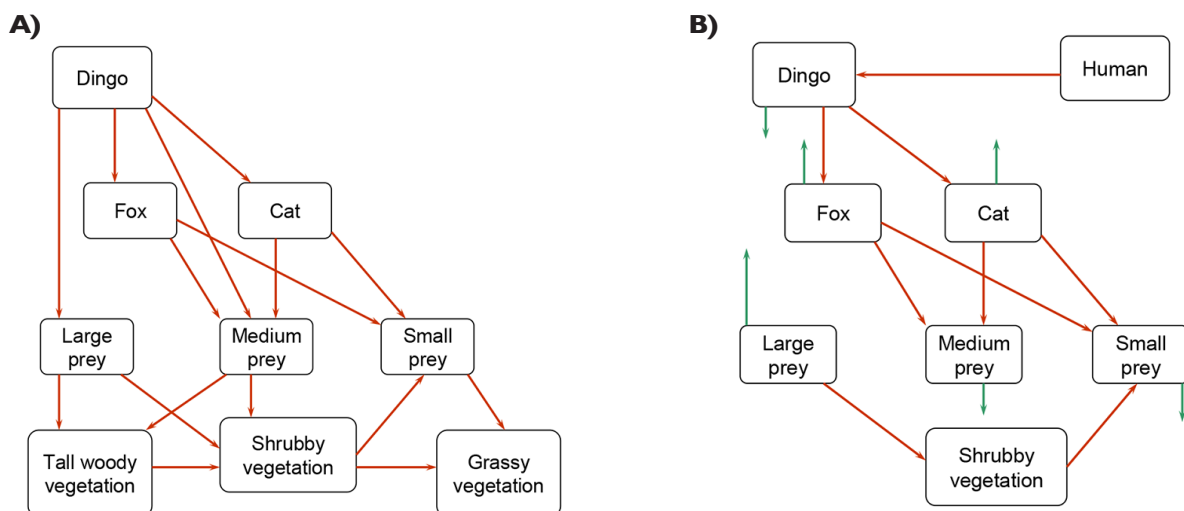
The dingo is often referred to as Australia's apex predator (e.g., Dickman *et al.* 2009; Fillios *et al.* 2010; Letnic *et al.* 2013) and there is widespread support for this concept and for meso-predator release hypothesis (e.g., Letnic *et al.* 2011; Ripple *et al.* 2014; Ritchie *et al.* 2012). However, dingoes can only be top-order predators in the absence of people. As we have stated before (Fleming *et al.* 2012),



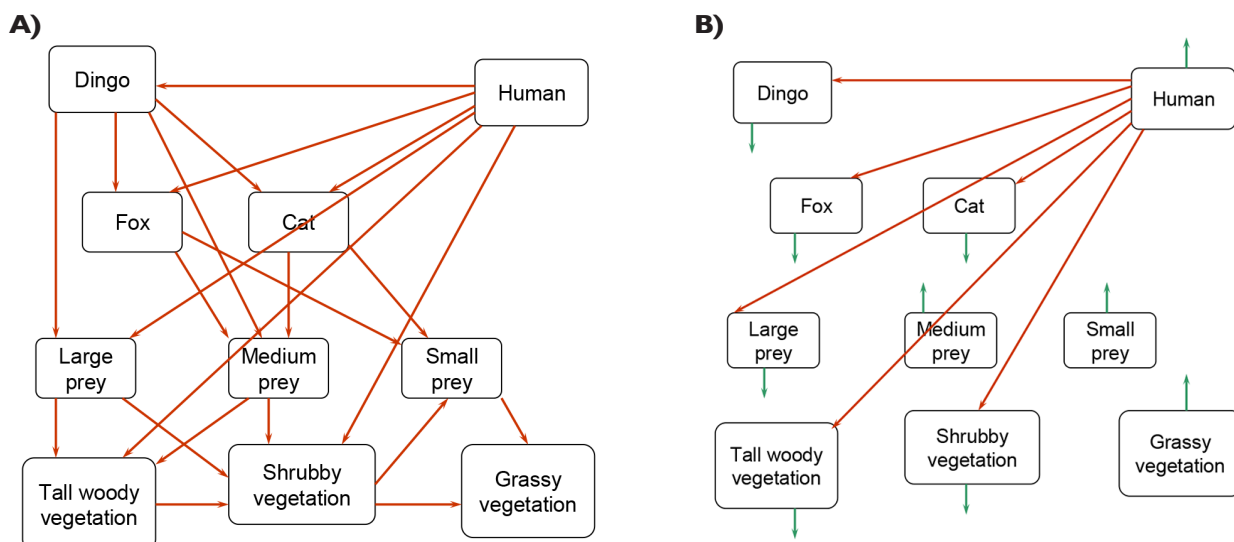
**Fig 1** Human suppression of dingoes and other wild dogs in the North Coast and Tablelands Wild Dog Control Board district (annual number of scalps presented for bounty payment) from 1946 to 1986, when scalp bounties ceased. Before aerial baiting, control was mostly undertaken by trappers (Harden and Robertshaw 1987). Aerial baiting commenced in 1966 on the Tablelands and in 1967 on the North Coast; scalp records were cumulative over 12 months.

humans are the top-order predator in Australia; we regulate ungulates in the various agri-ecosystems and have facilitated the extinction of perceived competitors, such as the dingo in much of the sheep/ wheat belt of eastern Australia and the thylacine (*Thylacine cynocephalus*) in Tasmania. In other ecosystems, we have facilitated dingoes through resource subsidies including domestic ungulates (Allen and West 2013; Allen and Fleming 2004), water and rubbish (Newsome *et al.* 2013). Suppression of dingo populations by human control actions (which is functionally equivalent to predation, Caughley and Sinclair 1994) has been demonstrated (Harden and Robertshaw 1987; and Fig 1). So, dingoes and other wild

dogs are our mesopredators, which is a descriptive rather than derogatory term. We are not redefining dingoes as mesopredators because they have always filled that descriptive niche (Buskirk 1999; Fleming *et al.* 2012); they are much closer in size to mesopredator coyotes (*Canis latrans*) than grey wolves (*Canis lupus*), which are often considered apex in North American systems (e.g. Ripple *et al.* 2014), and have always been preyed upon by humans, both in their native Asia and in Australia (Corbett 2001). This is implicit in papers suggesting humans stop preying upon dingoes to release them from suppression (e.g., Colman *et al.* 2014; Wallach *et al.* 2010; Wallach *et al.* 2009): if it were not so, our control actions would not



**Fig 2.** A) A schema of possible trophic suppressive effects in Australian ecosystems ignoring humans. B) A schema of possible tri-trophic response to human predation of dingoes only. Red arrows are suppressive effects and green arrows are directions of expected population size change when suppression is removed.

*Homo sapiens* is the apex animal

**Fig 3.** A) A schema of some trophic suppressive effects including humans, showing greater complexity. B) One alternative schema of trophic responses to some anthropogenic influences, including lethal control of dingoes, foxes, cats and kangaroos, and tree and shrub clearing. Red arrows are suppressive effects and green arrows show expected direction of trophic responses.

matter. The consequence of a shift in focus to humans as apex predators is that we have multi-trophic ecosystems (e.g. Figs 2 and 3), which are not as amenable to hypothesised mesopredator release processes as tri-trophic systems (Ekerholm *et al.* 2004; Oksanen *et al.* 1981). This could partly explain why tri-trophic cascades have not been demonstrated experimentally in Australian systems (Allen *et al.* 2013a; Allen *et al.* 2013b). Mesopredator release can be observed in wild canid populations when suppression by humans is removed, and greater predation on ungulates (Fleming *et al.* 2014; Wicks and Allen 2012) and macropods (Letnic and Crowther 2013; Pople *et al.* 2000) would be expected to result. Humans are also hypercarnivores, whose surplus killing facilitates mesopredator abundance by providing waste (Newsome *et al.* 2014; Newsome *et al.* 2013).

The consequences of anthropogenically subsidised mesopredator density for smaller prey and vegetation, alluded to by Colman *et al.* (2014), are uncertain and require experimental manipulations to test the mesopredator release hypothesis and trophic cascading effects (Allen *et al.* 2013a; Ritchie *et al.* 2012). This can be done by exerting human predation on wild canids in a controlled and replicated design (e.g. Arthur *et al.* 2012) and as is being done in the biodiversity hotspot of north east NSW (Fleming *et al.* 2006; Ballard *et al.* 2014). There, the effects of human predation targeting dingoes and other wild dogs are being measured for wild dogs, red foxes, feral cats, and spotted-tailed quolls (*Dasyurus maculatus*), herbivores and vegetation.

### Restorative actions in the presence of anthropocentric humans

How, then, does this discussion influence decisions for

biodiversity conservation and restoration? Firstly, we must embrace the anthropocentric reality of our world to make a difference to it. We are not saying “like it”; we are saying, “let’s acknowledge and address it explicitly”. This is essentially a simple adaptive management process (e.g., Chapple *et al.* 2011; Kingsford *et al.* 2011; Walters and Holling 1990) that incorporates human dimensions during the problem definition and management action phases. People are a (the) serious problem; they must be a big part of the solution if we are to reconcile faunal biodiversity conservation with human uses of landscapes (Cullen-Unsworth *et al.* 2012; Sayer *et al.* 2013). Humans are the apex consumers of predators, prey and vegetation. Perversely, anthropocentrism leads to an unrealistic desire for people to ‘step out’ so that we can return systems to pristine, untouched landscapes or wilderness, as if that is some static display in a large outdoor museum. As apex consumers aiming to achieve ecological and economic sustainability, we must ‘manage’ to minimise and mitigate the negative impacts of our consumption; they will never be zero. Although most scientists implicitly or explicitly acknowledge the massive roles that humans play at all levels from biome to niche, it sometimes seems to us that the human element is taken as a given and then omitted from descriptive models..

Secondly, when proposing remedial actions for biodiversity conservation, we must not assume that hypotheses ignoring humans as apex consumers prevail and then promptly cease top-down forcing upon systems, as has been suggested (e.g., Ritchie *et al.* 2012; Wallach *et al.* 2010). Considering this, we revise Estes *et al.* (2011, p306) provocative statement to, “The burden of proof [should, our insertion] be shifted to show, for any ecosystem, that consumers [including humans, our insertion] do (or did) not exert strong cascading effects”. When Letnic *et al.* (2013) reaffirmed the intent of Estes’ original statement for Australian conditions, they presupposed that dingoes

would be able to exert the same top-down forcing on red foxes and feral cats that humans could. Anthropogenic impacts are inherently tied to conservation targets (*sensu* Hayward 2012). The importance of anthropogenic top-down forcing through predator control and fencing to enable recovery of threatened species (Hayward 2012; Hayward and Kerley 2009) is implicit in the private and private-public conservation projects, such as Australian Wildlife Conservancy (Woinarski *et al.* 2011) and Bush Heritage (Figgis *et al.* 2005) restorations.

Thirdly, immediate and delayed anthropogenic influences on biodiversity are only likely to increase along with human population size and demand for resources. Human resource needs and uses have to be incorporated in models and their testing. Future impacts caused by climate change include fragmentation and loss of montane ecosystems and some associated species, severe drying and reductions in water resources in southern Australia, increased heatwaves, fire frequency and intensity and increased damage to ecosystems through these factors (Reisinger *et al.* 2014). We argue that our chances of rejuvenating ecosystems are limited by ignoring human roles in most environments, whether they be widespread ecosystem engineering through climate change, indirect impacts by providing resource subsidies to predators and their prey, or direct impacts through predation on predators.

The importance of human activities in modifying trophic cascades has been shown (e.g., human presence affects wolf space use, with effects on elk (*Cervus elaphus*) and beaver (*Castor canadensis*) abundance in Banff National Park, Canada; Hebblewhite *et al.* 2005; and see Estes *et al.* 2011 for a good review). Trophic models that ignore historical and contemporary human influence cannot adequately describe or predict system functions and the results of such models should never be used to proscribe management actions. They're not just likely to be wrong, but are ultimately useless and possibly damaging.

Seeking to recover or reintroduce animals must be done with an explicit recognition that humans will always be in or influence the systems. Ecosystems will not be returning to a pre-European, let alone pre-human, situation anytime soon. Zoologists and ecologists should recognise that humans are important in what happens to fauna and human needs must be considered when managing to sustain fauna (Brown 2009). Restoration of faunal assemblages requires understanding of threats, which in turn requires that all the terms, including anthropogenic changes, are included in models and experiments. Otherwise, all is argument without hope of resolution and appropriate action.

## Conclusion

Humans exert great power over most, if not all, ecosystems on earth. The "Sword of Damocles is

hanging over [our] head" (O'Brien 1973), and is often used to allude to the peril, anxiety and responsibility that come with power. We have the power and responsibility to make decisions affecting ecosystems but often with insufficient or incorrect information because human impacts and history have been omitted from the models.

Ignoring human impacts (i.e., the humans in the room), that is, climate change, land and water change or degradation, or anthropogenic trophic cascades, stymies our chances of maintaining or rejuvenating ecosystems or enhancing faunal biodiversity. This must occur while ensuring human resource needs are met, including agricultural production. In our opinion, based on perusal of contemporary ecological literature, many ecologists take humans as a given cause of ecological woes, and promptly ignore their roles as apex predator and ultimate ecosystem engineers while developing their argument (e.g., Dickman *et al.* 2009; Estes *et al.* 2011; Letnic *et al.* 2013). This leads to the undertaking of research as if humans had no historical or ongoing influence on the system of interest. It should be obvious that such thinking is restrictive when developing understanding of how systems operate in the ubiquitous presence of humans. *A priori* hypotheses should allow for alternative explanations, including the history of human interventions. Where the underlying conditions differ, treatment differences may just reflect starting point differences rather than treatment effects. To test for differences the influence of season, habitat and prior management should be similar across sites.

"Essentially, all models are wrong, but some are useful" (Box and Draper 1987). We add that some models are more wrong than others and that models that omit major components are useless. We posit that there are very few places in Australia where humans have not had or are not currently having impacts on the functioning of ecosystems. By leaving historical and current human impacts (accumulated over >45,000 years and exacerbated in the past 225 years) out of the models, we cannot adequately describe or predict system functions. The consequence for conservation is that recovery actions suggested for systems where humans are ignored are more likely to be ineffective. *A priori* hypotheses should allow for alternative explanations, including the history of human interventions and the currency of human occupation and activities. Threatening processes will not be found if human effects are excluded from the models. In the Anthropocene epoch in which we live, we must take the responsibility that comes with the power at the apex; we do not have the option of fleeing.

## Acknowledgements

We acknowledge the support of the Invasive Animals

*Homo sapiens* is the apex animal

Cooperative Research Centre, and Bob Harden, Brian Ferris and Bruce Moore for providing data. Discussions with members of the UNE Dog Empire, Paul Meek,

John Tracey, Sam Doak and Ben Allen helped in

developing these ideas. Hugh Fleming edited the manuscript, and Peter Banks and two anonymous reviewers provided valuable comments.

## References

- Abbott, I. 2002 Origin and spread of the cat, *Felis catus*, on mainland Australia, with a discussion of the magnitude of its early impact on native fauna. *Wildlife Research* 29: 51-74. <http://dx.doi.org/10.1071/WR01011>
- Allen, B., Allen, L., Engeman, R. and Leung, L.K.P. 2013a Intraguild relationships between sympatric predators exposed to lethal control: predator manipulation experiments. *Frontiers in Zoology* 10: 39. <http://dx.doi.org/10.1186/s12983-014-0056-y>
- Allen, B. L. and West, P. 2013 Influence of dingoes on sheep distribution in Australia. *Australian Veterinary Journal* 91: 261-267. <http://dx.doi.org/10.1111/avj.12075>
- Allen, B. L. 2011 A comment on the distribution of historical and contemporary livestock grazing across Australia: Implications for using dingoes for biodiversity conservation. *Ecological Management & Restoration* 12: 26-30. <http://dx.doi.org/10.1111/j.1442-8903.2011.00571.x>
- Allen, B. L., Fleming, P. J. S., Allen, L. R., Engeman, R. M., Ballard, G. and Leung, L. K.-P. 2013b As clear as mud: A critical review of evidence for the ecological roles of Australian dingoes. *Biological Conservation* 159: 158-174. <http://dx.doi.org/10.1016/j.biocon.2012.12.004>
- Allen, L. R. and Fleming, P. J. S. 2004 Review of canid management in Australia for the protection of livestock and wildlife - potential application to coyote management. *Sheep and Goat Research Journal* 19: 97-104. <http://digitalcommons.unl.edu/icwds/sheepgoat/2>
- Archer, S. 2000 Technology and ecology in the Karoo: a century of windmills, wire and changing farming practice. *Journal of Southern African Studies* 26: 675-696. <http://dx.doi.org/10.1080/03057070020008224>
- Arthur, A.D., Catling, P.C. and Reid, A. 2012 Relative influence of habitat structure, species interactions and rainfall on the post-fire population dynamics of ground-dwelling vertebrates. *Austral Ecology* 37: 958-970. <http://dx.doi.org/10.1111/j.1442-9993.2011.02355.x>
- Atkinson, J. 1826 An Account of the State of Agriculture and Grazing in New South Wales. J Cross, Holborn, UK.
- Australian Bureau of Statistics 2009 Table 6 Sheep. In Australian Agricultural Census, 71240DO001-200708: Historical Selected Agricultural Commodities, by State (1861 to Present), 2009. Australian Bureau of Statistics, Canberra, ACT.
- Australian Bureau of Statistics 2012 3235.0 Population by age and sex, regions of Australia, 2012. Australian Bureau of Statistics, Canberra, ACT.
- Australian Bureau of Statistics 2014 Australian Population Clock. Australian Bureau of Statistics, Canberra, ACT.
- Ballard, G., Fleming, P., Melville, G., Pradhan, U., Payne, N., Russell, B. and Theakston, P. 2011 Feral Goat Population Trends in Western New South Wales Rangelands. NSW Department of Primary Industries, Orange, NSW.
- Ballard, G., Meek, P.D., Doak, S., Fleming, P.J.S. and Sparkes, J. 2014 Camera traps, sand plots and known events: what do camera traps miss? Pp. 189-202 In. Camera Trapping for Wildlife Management and Research, editors P. Meek, P. Fleming, G. Ballard, P. Banks, A. Claridge, J. Sanderson and D. Swann. CSIRO Publishing, Australasian Wildlife Management Society, Royal Zoological Society of NSW, Collingwood, Vic.
- Bauer, E.H. 1962 Sheep-raising in northern Australia: A historical review. Pp. 457-471 in The Simple Fleece: Studies in the Australian Wool Industry, edited by A. Barnard. Melbourne University Press, Melbourne, Vic.
- Bauer, J. J. and Giles, J. 2002 Recreational Hunting: an International Perspective. CRC for Sustainable Tourism, Canberra, ACT.
- Bird, M. I., Hutley, L. B., Lawes, M.J., Lloyd, J., Luly, J. G., Ridd, P. V., Roberts, R. G., Ulm, S. and Wurster, C. M. 2013 Humans, megafauna and environmental change in tropical Australia. *Journal of Quaternary Science* 28: 439-452. <http://dx.doi.org/10.1002/jqs.2639>
- Bird, P., Mutze, G., Peacock, D. and Jennings, S. 2012 Damage caused by low-density exotic herbivore populations: the impact of introduced European rabbits on marsupial herbivores and *Allocasuarina* and *Bursaria* seedling survival in Australian coastal shrubland. *Biological Invasions* 14: 743-755. <http://dx.doi.org/10.1007/s10530-011-0114-8>
- Box, G. E. P. and Draper, N. R. 1987 *Empirical Model Building and Response Surfaces*. John Wiley & Sons, New York, USA.
- Brockerhoff, E. G., Jactel, H., Parrotta, J. A., Quine, C. P. and Sayer, J. 2008 Plantation forests and biodiversity: oxymoron or opportunity? *Biodiversity and Conservation* 17: 925-951. <http://dx.doi.org/10.1007/s10531-008-9380-x>
- Brown, P.J. 2009 Introduction: Perspectives on the past and

- future of human dimensions of fish and wildlife. Pp. 1-13 in *Wildlife and Society: The Science of Human Dimensions*, edited by M.J. Manfredo, J.J. Vaske, P.J. Brown, D.J. Decker and E.A. Duke. Island Press, Washington, USA.
- Burbidge, A. A., McKenzie, N. L., Brennan, K. E. C., Woinarski, J. C. Z., Dickman, C. R., Baynes, A., Gordon, G., Menkhorst, P. W. and Robinson, A. C. 2008 Conservation status and biogeography of Australia's terrestrial mammals. *Australian Journal of Zoology* 56: 411-422. <http://dx.doi.org/10.1071/ZO08027>
- Buskirk, S.W. 1999 Mesocarnivores of Yellowstone. Pp. 165-187 in *Carnivores in Ecosystems: the Yellowstone Experience*, edited by T.W. Clark, A.P. Curlee, S.C. Minta and P.M. Kareiva. Yale University Press, New Haven, USA.
- Butlin, N.G. 1962 Distribution of the sheep population: Preliminary statistical picture, 1860-1957. Pp. 281-307 in *The Simple Fleece: Studies in the Australian Wool Industry*, edited by A. Barnard. Melbourne University Press, Parkville, Vic.
- Caughley, G and Grigg, G.C. 1982 Numbers and distribution of kangaroos in the Queensland pastoral zone. *Wildlife Research* 9: 365-371. <http://dx.doi.org/10.1071/WR9820365>
- Caughley, G. 1986. Rangelands, livestock and wildlife, the ecological equivalent of sulphur, saltpetre and charcoal. Pp. 545 in *Rangelands: a Resource Under Siege*. Proceedings of the second International Rangeland Congress, edited by P.J. Joss, P.W. Lynch and O.B. Williams. Australian Academy of Science, Canberra, ACT.
- Caughley, G., Grigg, G. C., Caughley, J. and Hill, G. J. E. 1980. Does dingo predation control the densities of kangaroos and emus? *Australian Wildlife Research* 7: 1-12. <http://dx.doi.org/10.1071/WR9800001>
- Caughley, G. and Sinclair, A. R. E. 1994. *Wildlife Ecology and Management*. Blackwell Science, Cambridge, Massachusetts, USA.
- Chapple, R. S., Ramp, D., Bradstock, R. A., Kingsford, R. T., Merson, J. A., Auld, T. D., Fleming, P. J.S. and Mulley, R. C. 2011. Integrating science into management of ecosystems in the Greater Blue Mountains. *Environmental Management* 48: 659-674. <http://dx.doi.org/10.1007/s00267-011-9721-5>
- Choquenot, D. and Forsyth, D. M. 2013. Exploitation ecosystems and trophic cascades in non-equilibrium systems: pasture – red kangaroo – dingo interactions in arid Australia. *Oikos* 122: 1292-1306. <http://dx.doi.org/10.1111/j.1600-0706.2012.20976.x>
- Colman, N. J., Gordon, C. E., Crowther, M. S. and Letnic, M. 2014. Lethal control of an apex predator has unintended cascading effects on forest mammal assemblages. *Proceedings of the Royal Society B: Biological Sciences* 281: 20133094 <http://dx.doi.org/10.1098/rspb.2013.3094>.
- Coman, B.J. 1999. *Tooth & Nail: the Story of the Rabbit in Australia*. Text Publishing, Melbourne, Vic.
- Corbett, L. K. 2001. *The Dingo in Australia and Asia. Second Edition*. JB Books Australia, Marleston, Vic.
- Croft, J.D., Fleming, P.J.S. and van de Ven, R. 2002. The impacts of rabbits on a grazing system in eastern New South Wales. 1. ground cover and pastures. *Australian Journal of Experimental Agriculture* 42: 909-916. <http://dx.doi.org/10.1071/EA01106>
- Crutzen, P.J. 2006. The "Anthropocene". Pp. 13-18 in *Earth System Science in the Anthropocene*, edited by E. Ehlers and T. Krafft. Springer, Heidelberg, Germany
- Cullen-Unsworth, L.C., Hill, R., Butler, J.R.A. and Wallace, M. 2012. A research process for integrating Indigenous and scientific knowledge in cultural landscapes: principles and determinants of success in the Wet Tropics World Heritage Area, Australia. *The Geographical Journal* 178: 351-365. <http://dx.doi.org/10.1111/j.1475-4959.2011.00451.x>
- Denham, A. J. and Auld, T. D. 2004. Survival and recruitment of seedlings and suckers of trees and shrubs of the Australian arid zone following habitat management and the outbreak of Rabbit Calicivirus Disease (RCD). *Austral Ecology* 29: 585-599. <http://dx.doi.org/10.1111/j.1442-9993.2004.01393.x>
- Derry, J.E. 2004. Piospheres in semi-arid rangeland: consequences of spatially constrained plant-herbivore interactions. University of Edinburgh, Edinburgh, UK.
- Dickman, C., Glen, A. and Letnic, M. 2009. Reintroducing the dingo: Can Australia's conservation wastelands be restored? Pp. 238-269 in *Reintroduction of Top-order Predators*, edited by M.W. Hayward and M.J. Somers. Wiley-Blackwell, Oxford, UK.
- Ekerholm, P., Oksanen, L., Oksanen, T. and Schneider, M. 2004. The impact of short-term predator removal on vole dynamics in an arctic-alpine landscape. *Oikos* 106: 457-468. <http://dx.doi.org/10.1111/j.0030-1299.2004.12639.x>
- Eldridge, D.J. and Simpson, R. 2002. Rabbit (*Oryctolagus cuniculus* L.) impacts on vegetation and soils, and implications for management of wooded rangelands. *Basic and Applied Ecology* 3: 19-29.
- Estes, J.A., Terborgh, J., Brashares, J.S., Power, M.E., Berger, J., Bond, W.J., Carpenter, S.R., Essington, T.E., Holt, R.D., Jackson, J.B.C., Marquis, R.J., Oksanen, L., Oksanen, T., Paine, R.T., Pikitch, E.K., Ripple, W.J., Sandin, S.A., Scheffer, M., Schoener, T.W., Shurin, J.B., Sinclair, A.R.E., Soulé, M.E., Virtanen, R. and Wardle, D.A. 2011 Trophic downgrading of planet earth. *Science* 333: 301-306. <http://dx.doi.org/10.1126/science.1205106>
- Evans, J. V. 1980. The Angora-mohair industry in Australia. Part 1. An historical perspective. Pp. 69-86 in *Proceedings of*

*Homo sapiens* is the apex animal

- the Post-Graduate Committee in Veterinary Science, University of Sydney, edited by Post-Graduate Committee in Veterinary Science. University of Sydney, Camperdown, NSW.
- Fensham, R.J. and Fairfax, R.J.** 2008. Water-remoteness for grazing relief in Australian arid-lands. *Biological Conservation* 141: 1447-1460. <http://dx.doi.org/10.1016/j.biocon.2008.03.016>
- Figgis, P., Humann, D. and Looker, M.** 2005. Conservation on private land in Australia. *Parks* 15: 19-29.
- Fillios, M., Gordon, C., Koch, F. and Letnic, M.** 2010. The effect of a top predator on kangaroo abundance in arid Australia and its implications for archaeological faunal assemblages. *Journal of Archaeological Science* 37: 986-993. <http://dx.doi.org/doi:10.1016/j.jas.2009.11.031>
- Fleischner, T.L.** 1994. Ecological costs of livestock grazing in western North America. *Conservation Biology* 8: 629-644.
- Fleming, P.J.S., Allen, B.L., Allen, L.R., Ballard, G., Bengsen, A.J., Gentle, M.N., McLeod, L.J., Meek, P.D. and Saunders, G.R.** 2014. Management of wild canids in Australia: free-ranging dogs and red foxes. Pp 105-149, In *Carnivores of Australia: Past, Present and Future*, edited by A.S. Glen and C.R. Dickman. CSIRO Publishing, Collingwood., Vic.
- Fleming, P. J. S., Allen, B. L. and Ballard, G-A.** 2012. Seven considerations about dingoes as biodiversity engineers: the socioecological niches of dogs in Australia. *Australian Mammalogy* 34: 119-131. <http://dx.doi.org/10.1071/AM11012>
- Fleming, P.J.S., Allen, L.R., Lapidge, S.J., Robley, A., Saunders, G.R. and Thomson, P.C.** 2006. A strategic approach to mitigating the impacts of wild canids: proposed activities of the Invasive Animals Cooperative Research Centre. *Australian Journal of Experimental Agriculture* 46: 753-762. <http://dx.doi.org/10.1071/EA06009>
- Fleming, P.J.S., Limin, Hua and Whisson, D.C.** 2013. Impacts and management of invasive burrowing herbivores in grasslands. Pp. 1600-1608 in *Revitalising Grasslands to Sustain Our Communities: Proceedings of the 22nd International Grassland Congress*, edited by D.L. Michalk, G.D. Millar, W.B. Badgery and K.M. Broadfoot. NSW Department of Primary Industries, Orange, NSW.
- Gamage, B.** 2011. *The Biggest Estate on Earth: How Aborigines Made Australia*. Allen & Unwin, Sydney, NSW.
- Gill, A. M. and Williams, J.E.** 1996. Fire regimes and biodiversity: the effects of fragmentation of southeastern Australian eucalypt forests by urbanisation, agriculture and pine plantations. *Forest Ecology and Management* 85: 261-278.
- Hacker, R. and McLeod, S.** 2003. *Living With Kangaroos: A Guide to Kangaroos and Their Management in the Murray-Darling Basin*. State of New South Wales, NSW Agriculture, Orange, NSW.
- Harden, R.H. and Robertshaw, J. D.** 1987. The ecology of the dingo in north-eastern New South Wales. V. Human predation on the dingo. *Australian Zoologist* 24: 65-72.
- Harrington, G. N., Chantler, D., Henzell, R., Holst, P. J., McRae, I., Mahood, I., Mitchell, T. D., O'Brien, P. H., Snowdon, W. A. and Hein, W. R.** 1982. Chapter 1: The feral goat. Pp. 1-73 in *Goats for Meat and Fibre in Australia: Report of the Expert Panel Appointed by the Animal Production Committee of Standing Committee on Agriculture*, edited by P.J. Holst. CSIRO, Canberra, ACT.
- Hayward, M.W., Kerley, G.I.H., Adendorff, J., Moolman, L.C., O'Brien, J., Sholto-Douglas, A., Bissett, C., Bean, P., Fogarty, A., Howarth, D. and Slater, R.** 2007. The reintroduction of large carnivores to the Eastern Cape, South Africa: an assessment. *Oryx* 41:205-214. <http://dx.doi.org/10.1017/S0030605307001767>
- Hayward, M.W.** 2012. Time to agree on a conservation benchmark for Australia. *Pacific Conservation Biology* 18: 69-76. <http://dx.doi.org/10.1071/PC120069>
- Hayward, M.W. and Kerley, G.I.H.** 2009. Fencing for conservation: Restriction of evolutionary potential or a riposte to threatening processes? *Biological Conservation* 142, 1-13. <http://dx.doi.org/10.1016/j.biocon.2008.09.022>
- Hebblewhite, M., White, C.A., Nietvelt, C.G., McKenzie, J.A., Hurd, T.E., Fryxell, J.M., Bayley, S.E. and Paquet, P.C.** 2005. Human activity mediates a trophic cascade caused by wolves. *Ecology* 86: 2135-2144. <http://dx.doi.org/10.1890/04-1269>
- Hobbs, R.J., Arico, S., Aronson, J., Baron, J.S., Bridgewater, P., Cramer, V.A., Epstein, P.R., Ewel, J.J., Klink, C.A., Lugo, A.E., Norton, D., Ojima, D., Richardson, D.M., Sanderson, E.W., Valladares, E., Vilà, M., Zamora, R. and Zobel, M.** 2006. Novel ecosystems: theoretical and management aspects of the new ecological world order. *Global Ecology and Biogeography* 15: 1-7. <http://dx.doi.org/10.1111/j.1466-822X.2006.00212.x>
- Holt, J.A.** 1997. Grazing pressure and soil carbon, microbial biomass and enzyme activities in semi-arid northeastern Australia. *Applied Soil Ecology* 5: 143-149.
- Hunt, L.P., Petty, S., Cowley, R., Fisher, A., Ash, A.J. and MacDonald, N.** 2007. Factors affecting the management of cattle grazing distribution in northern Australia: preliminary observations on the effect of paddock size and water points. *The Rangeland Journal* 29: 169-179. <http://dx.doi.org/10.1071/RJ07029>
- Jackson, S.M. and Groves, C.P.** 2015. *Taxonomy of Australian Mammals*. CSIRO Publishing, Melbourne, Vic.
- Jenkins, D.J., Romig, T. and Thompson, R.C.A.** 2005. Emergence/re-emergence of *Echinococcus* spp.—a global update. *International Journal for Parasitology* 35: 1205-1219. <http://dx.doi.org/10.1016/j.ijpara.2005.07.014>

- Johnson, C. 2006. *Australia's Mammal Extinctions: A 50 000 Year History*. Cambridge University Press, Melbourne, Vic.
- Jonzen, N., Pople, T., Knape, J. and Skold, M. 2010. Stochastic demography and population dynamics in the red kangaroo *Macropus rufus*. *Journal of Animal Ecology* 79: 109-116. <http://dx.doi.org/10.1111/j.1365-2656.2009.01601.x>
- Kingsford, R.T., Biggs, H.C. and Pollard, S.R. 2011. Strategic adaptive management in freshwater protected areas and their rivers. *Biological Conservation* 144: 1194-1203. <http://dx.doi.org/10.1016/j.biocon.2010.09.022>
- Lange, R. T. 1969. The piosphere: sheep track and dung patterns. *Journal of Range Management* 22: 396-400. <http://www.jstor.org/stable/3895849>
- Lapidge, S.J. and Henshall, S. 2001. Diet of foxes and cats, with evidence of predation on yellow-footed rock-wallabies (*Petrogale xanthopus* Celeris) by foxes in South western Queensland. *Australian Mammalogy* 23: 47-52. <http://dx.doi.org/10.1071/AM01047>
- Legge, S., Kennedy, M.S., Lloyd, R., Murphy, S.A. and Fisher, A. 2011. Rapid recovery of mammal fauna in the central Kimberley, northern Australia, following the removal of introduced herbivores. *Austral Ecology* 36: 791-799. <http://dx.doi.org/10.1111/j.1442-9993.2010.02218.x>
- Lethbridge, M.R. and Alexander, P.J. 2008. Comparing population growth rates using weighted bootstrapping: Guiding the conservation management of *Petrogale xanthopus xanthopus* (yellow-footed rock-wallaby). *Biological Conservation* 141: 1185-1195. <http://dx.doi.org/10.1016/j.biocon.2007.09.026>
- Letnic, M. 2000. Dispossession, degradation and extinction: environmental history in arid Australia. *Biodiversity and Conservation* 9: 295-308. <http://dx.doi.org/10.1023/A:1008913826686>
- Letnic, M., Baker, L. and Nesbitt, B. 2013. Ecologically functional landscapes and the role of dingoes as trophic regulators in south-eastern Australia and other habitats. *Ecological Management and Restoration* 14: 101-105. <http://dx.doi.org/10.1111/emr.12035>
- Letnic, M. and Crowther, M. S. 2013. Patterns in the abundance of kangaroo populations in arid Australia are consistent with the exploitation ecosystems hypothesis. *Oikos* 122: 761-769. <http://dx.doi.org/10.1111/j.1600-0706.2012.20425.x>
- Letnic, M., Crowther, M.S. and Koch, F. 2009. Does a top-predator provide an endangered rodent with refuge from an invasive mesopredator? *Animal Conservation* 12: 302-312. <http://dx.doi.org/10.1111/j.1469-1795.2009.00250.x>
- Letnic, M. and Dworjanyn, S. A. 2011. Does a top predator reduce the predatory impact of an invasive mesopredator on an endangered rodent? *Ecography* 34: 827-835. <http://dx.doi.org/10.1111/j.1600-0587.2010.06516.x>
- Letnic, M. and Koch, F. 2010. Are dingoes a trophic regulator in arid Australia? A comparison of mammal communities on either side of the dingo fence. *Austral Ecology* 35: 167-175. <http://dx.doi.org/10.1111/j.1442-9993.2009.02022.x>
- Letnic, M., Ritchie, E. G. and Dickman, C. R. 2011. Top predators as biodiversity regulators: the dingo *Canis lupus dingo* as a case study. *Biological Reviews* 87: 390-413. <http://dx.doi.org/10.1111/j.1469-185X.2011.00203.x>
- Linnell, J.D.C., Swenson, J.E. and Anderson, R. 2001. Predators and people: conservation of large carnivores is possible at high human densities if management policy is favourable. *Animal Conservation* 4: 345-349. <http://dx.doi.org/10.1017/S1367943001001408>
- Lunney, D. 2001. Causes of the extinction of native mammals of the Western Division of New South Wales: an ecological interpretation of the nineteenth century historical record. *The Rangeland Journal* 23: 44-70. <http://dx.doi.org/10.1071/RJ01014>
- Lunney, D. 2010. A history of the debate (1948-2009) on the commercial harvesting of kangaroos, with particular reference to New South Wales and the role of Gordon Grigg. *Australian Zoologist* 35: 383-430. <http://dx.doi.org/10.7882/AZ.2010.027>
- Lunney, D., Gresser, S., O'Neill, L.E, Matthews, A. and Rhodes, J. 2007. The impact of fire and dogs on koalas at Port Stephens, New South Wales, using population viability analysis. *Pacific Conservation Biology* 13: 189-201. <http://dx.doi.org/10.1071/PC070189>
- McLeod, S.R., Hacker, R.B. and Druhan, J.P. 2004. Managing the commercial harvest of kangaroos in the Murray-Darling Basin. *Australian Mammalogy* 26: 9-22. <http://dx.doi.org/10.1071/AM04009>
- Meek, P.D. and Triggs, B. 1998. The food of foxes, dogs and cats on two peninsulas in Jervis Bay, New South Wales. *Proceedings of the Linnean Society of NSW* 120: 117-127.
- Moyal, A. 2008. *Koala: a Historical Biography*. CSIRO Publishing, Collingwood, Vic.
- Mutze, G., Bird, P., Cooke, B. and Henzell, R. 2008. Geographic and seasonal variation in the impact of rabbit haemorrhagic disease on European rabbits, *Oryctolagus cuniculus*, and rabbit damage in Australia. Pp. 279-293 in *Lagomorph Biology*, edited by P. Alves, N. Ferrand and K. Hackländer. Springer Berlin, Heidelberg, Germany.
- Newsome, A. E., Catling, P. C., Cooke, B. D. and Smyth, R. 2001. Two ecological universes separated by the Dingo Barrier fence in semi-arid Australia: Interactions between landscapes, herbivory and carnivory, with and without dingoes. *The Rangeland Journal* 23: 71-98. <http://dx.doi.org/10.1071/RJ01015>

*Homo sapiens* is the apex animal

- Newsome, T.M., Ballard, G.-A., Fleming, P.J.S., van de Ven, R., Story, G.L. and Dickman, C.R. 2014 .Human-resource subsidies alter the dietary preferences of a mammalian top predator. *Oecologia* 175: 139-150. <http://dx.doi.org/10.1007/s00442-014-2889-7>
- Newsome, T.M., Ballard, G.-A., Dickman, C.R., Fleming, P.J. S. and Howden, C. 2013 .Anthropogenic resource subsidies determine space use by Australian arid zone dingoes: An improved resource selection modelling approach. *PLoS ONE* 8: e63931. <http://dx.doi.org/10.1371/journal.pone.0063931>
- Nugent, G. and Choquenot, D. 2004 .Comparing cost-effectiveness of commercial harvesting, state-funded culling, and recreational deer hunting in New Zealand. *Wildlife Society Bulletin* 32: 481-492. [http://dx.doi.org/10.2193/0091-7648\(2004\)32\[481:CCOCHS\]2.0.CO;2](http://dx.doi.org/10.2193/0091-7648(2004)32[481:CCOCHS]2.0.CO;2)
- O'Brien, R. 1973. The sword of damocles. In *The Rocky Horror Show*, produced by J. Sharman. Royal Court Theatre, Chelsea, UK.
- Oksanen, L., Fretwell, S.D., Arruda, J. and Niemala, P. 1981. Exploitation ecosystems in gradients of primary productivity. *American Naturalist* 118:240-261. <http://www.jstor.org/stable/2460513>
- Oskarsson, M.C.R., Klütsch, C.E.C., Boonyaparakob, U., Wilton, A., Tanabe, Y. and Savolainen, P. 2012. Mitochondrial DNA data indicate an introduction through mainland Southeast Asia for Australian dingoes and Polynesian domestic dogs. *Proceedings of the Royal Society B: Biological Sciences* 279: 967-974. <http://dx.doi.org/10.1098/rspb.2011.1395>
- Pang, J-F, Kluetsch, C., Zou, X-J., Zhang, A-B., Luo, L-Y., Angleby, H., Ardalan, A., Ekström, C., Skölleremo, A., Lundeberg, J., Matsumura, S., Leitner, T., Zhang, Y-P and Savolainen, P. 2009. mtDNA data indicate a single origin for dogs south of Yangtze River, less than 16,300 years ago, from numerous wolves. *Molecular Biology and Evolution* 26: 2849-2864. <http://dx.doi.org/10.1093/molbev/msp195>
- Pople, A. R., Grigg, G.C., Cairns, S.C., Beard, L. A. and Alexander, P. 2000. Trends in the numbers of red kangaroos and emus on either side of the South Australian dingo fence: evidence for predator regulation? *Wildlife Research* 27: 269-276. <http://dx.doi.org/10.1071/WR99030>
- Pople, A.R., Cairns, S.C. and McLeod, S.R. 2010. Increased reproductive success in older female red kangaroos and the impact of harvesting. *Australian Zoologist* 35: 160-165.
- Read, J. and Bowen, Z. 2001. Population dynamics, diet and aspects of the biology of feral cats and foxes in arid South Australia. *Wildlife Research* 28: 195-203. <http://dx.doi.org/10.1071/WR99065>
- Redford, K.H. and Sanderson, S. E. 2000. Extracting humans from nature. *Conservation Biology* 14: 1362-1364. <http://dx.doi.org/10.1046/j.1523-1739.2000.00135.x>
- Reisinger, A., Kitching, R. L., Chiew, F., Hughes, L., Newton, P., Schuster, S., Tait, A. and Whetton, P. 2014. Chapter 25: Australasia. Pp. 101 in *Climate change 2014: impacts, adaptation, and vulnerability, Fifth Assessment Report (AR5)*, edited by Intergovernmental Panel on Climate Change Working Group. United Nations Environment Program and World Meteorological Organization.
- Ripple, W.J., Estes, J.A., Beschta, R.L., Wilmers, C. C., Ritchie, E.G., Hebblewhite, M., Berger, J., Elmhagen, B., Letnic, M., Nelson, M.P., Schmitz, O.J., Smith, D.W., Wallach, A.D. and Wirsing, A.J. 2014. Status and Ecological Effects of the World's Largest Carnivores. *Science* 343: 6167, 1241484-1241484. <http://dx.doi.org/10.1126/science.1241484>
- Ritchie, E.G., Elmhagen, B., Glen, A.S., Letnic, M., Ludwig, G. and McDonald, R. A. 2012 Ecosystem restoration with teeth: what role for predators? *Trends in Ecology and Evolution* 27: 265-271. <http://dx.doi.org/10.1016/j.tree.2012.01.001>
- Rossiter, N.A., Setterfield, S.A., Douglas, M.M. and Hutley, L.B. 2003. Testing the grass-fire cycle: alien grass invasion in the tropical savannas of northern Australia. *Diversity and Distributions* 9: 169-176. <http://dx.doi.org/10.1046/j.1472-4642.2003.00020.x>
- Saunders, G., Coman, B., Kinnear, J. and Braysher, M. 1995. *Managing Vertebrate Pests: Foxes*. Australian Government Publishing Service, Canberra, ACT.
- Saunders, G., Kay, B., Mutze, G. and Choquenot, D. 2002. Observations on the impacts of rabbit haemorrhagic disease on agricultural production values in Australia. *Wildlife Research* 29: 605-613. <http://dx.doi.org/10.1071/WR00086>
- Saunders, G. R., Gentle, M.N. and Dickman, C. R. 2010. The impacts and management of foxes *Vulpes vulpes* in Australia. *Mammal Review* 40: 181-211. <http://dx.doi.org/10.1111/j.1365-2907.2010.00159.x>
- Savolainen, P., Leitner, T., Wilton, A. N., Matisoo-Smith, E. and Lundeberg, J. 2004. A detailed picture of the origin of the Australian dingo, obtained from the study of mitochondrial DNA. *Proceedings of the National Academy of Sciences of the United States of America* 101:12387-12390. <http://dx.doi.org/10.1073/pnas.0401814101>
- Sayer, J., Sunderland, T., Ghazoul, J., Pfund, J-L., Sheil, D., Meijaard, E., Venter, M., Boedhihartono, A.K., Day, M. and Garcia, C. 2013. Ten principles for a landscape approach to reconciling agriculture, conservation, and other competing land uses. *Proceedings of the National Academy of Sciences of the United States of America* 110: 8349-8356. <http://dx.doi.org/10.1073/pnas.1210595110>
- Smith, B. 1960. *European Vision and the South Pacific, 1768-1850*. Oxford University Press, London, UK.

- Thomsen, D.A. and Davies, J. 2005. Social and cultural dimensions of commercial kangaroo harvest in South Australia. *Animal Production Science* 45: 1239-1243. <http://dx.doi.org/10.1071/EA03248>
- Van De Koppel, J. and Rietkerk, M. 2000. Herbivore regulation and irreversible vegetation change in semi-arid grazing systems. *Oikos* 90: 253-260. <http://dx.doi.org/10.1034/j.1600-0706.2000.900205.x>
- Wallach, A.D., Johnson, C.N., Ritchie, E.G. and O'Neill, A.J. 2010. Predator control promotes invasive dominated ecological states. *Ecology Letters* 13: 1008-1018. <http://dx.doi.org/10.1111/j.1461-0248.2010.01492.x>
- Wallach, A.D. and O'Neill, A.J. 2009. Artificial water points: Hotspots of extinction or biodiversity? *Biological Conservation* 142: 1253-1254. <http://dx.doi.org/10.1016/j.biocon.2008.09.021>
- Wallach, A.D., Ritchie, E.G., Read, J. and O'Neill, A. 2009. More than mere numbers: the impact of lethal control on the social stability of a top-order predator. *PLoS One* 4: e6861. <http://dx.doi.org/10.1371/journal.pone.0006861>
- Walters, C. J. and Holling, C. S. 1990 Large-scale management experiments and learning by doing. *Ecology* 71: 2060-2068.
- West, P. 2008. Assessing Invasive Animals in Australia, 2008. National Land & Water Resources Audit and Invasive Animals Cooperative Research Centre, Canberra, ACT.
- Wicks, S. and Allen, B.L. 2012 Returns on Investment in Wild Dog Management: Beef Production in the South Australian Arid Lands. Australian Bureau of Agricultural and Resource Economics and Sciences, Department of Agriculture, Fisheries and Forestry, Canberra, ACT.
- Williams, C.K., Parer, I., Coman, B.J., Burley, J. and Braysher, M.L. 1995 *Managing Vertebrate Pests: Rabbits*. Bureau of Resource Sciences/CSIRO Division of Wildlife and Ecology, Australian Government Publishing Service, Canberra, ACT.
- Williams, O.B. 1962. The Riverina and its pastoral industry, 1860-1869. Pp. 411-434. In *The Simple Fleece: Studies in the Australian Wool Industry*, edited by A. Barnard. Melbourne University Press, Parkville, ACT.
- Wilson, G.R. and Edwards, M.J. 2008. Native wildlife on rangelands to minimize methane and produce lower-emission meat: kangaroos versus livestock. *Conservation Letters* 1:119-128. <http://dx.doi.org/10.1111/j.1755-263X.2008.00023.x>
- Woinarski, J. C. Z., Risler, J. and Kean, L. 2004. Response of vegetation and vertebrate fauna to 23 years of fire exclusion in a tropical Eucalyptus open forest, Northern Territory, Australia. *Austral Ecology* 29: 156-176. <http://dx.doi.org/10.1111/j.1442-9993.2004.01333.x>
- Woinarski, J. C. Z., Legge, S., Fitzsimons, J. A., Traill, B.J., Burbidge, A.A., Fisher, A., Firth, R.S. C., Gordon, I.J., Griffiths, A. D., Johnson, C. N., McKenzie, N.L., Palmer, C., Radford, I., Rankmore, B., Ritchie, E.G., Ward, S. and Ziemnicki, M. 2011. The disappearing mammal fauna of northern Australia: context, cause, and response. *Conservation Letters* 4:192-201. <http://dx.doi.org/10.1111/j.1755-263X.2011.00164.x>
- Woodroffe, R. 2000. Predators and people: using human densities to interpret declines of large carnivores. *Animal Conservation* 3:165-173. <http://dx.doi.org/10.1111/j.1469-1795.2000.tb00241.x>
- Wroe, S., Field, J., Fullagar, R. and Jermin, L.S. 2004. Megafaunal extinction in the late Quaternary and the global overkill hypothesis. *Alcheringa* 28: 291-331. <http://dx.doi.org/10.1080/03115510408619286>
- Zimmermann, A., Baker, N., Inskip, C., Linnell, J.D. C., Marchini, S., Odden, J., Rasmussen, G. and Treves, A. 2009. Contemporary views of human-carnivore conflicts on wild rangelands. Pp. 129-151 in *Wild Rangelands: Conserving Wildlife While Maintaining Livestock in Semi-arid Ecosystems*, edited by J. du Toit, R. Kock and J. Deutsch. Wiley-Blackwell, Hoboken, USA.